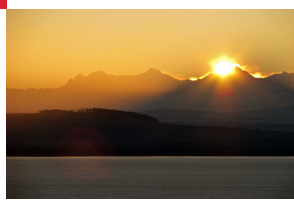

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6. Darwin, Evolution and Palaeontology

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6. Darwin, Evolution and Palaeontology

Lionel Cavin

Schweizerische Paläontologische Gesellschaft (SPG/SPS), Kommission der Schweizerischen Paläontologischen Abhandlungen (KSPA), Swiss Commission of Palaeontology Award

6.1

Late Aquitanian mammals from the Engehalde locality (Bern, Switzerland)

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Due to the construction of the Swiss national road from Bern to Worblaufen in 1850, the sandy and marly deposits of the Lower Freshwater Molasse (USM) were excavated in Engehalde. Some specimens of vertebrate fossils (turtles, ruminants, suids, and rhinocerotids) and shells of gastropods and bivalves were brought to light by Studer (1850). Then Stehlin (1914) reported the presence of *Palaeochoerus typus*, but the referred material was not found in the historical collection anymore. The same author notified also two ruminants, *Amphitragulus* cf. *elegans* and *Amphitragulus lemanense*. However, as these two taxa are considered synonyms, only *Amphitragulus elegens* is valid. Moreover, many specimens wrongly ascribed to *Amphitragulus elegans* or *Amphitragulus lemanense* in the literature have to be reported to the closer species *Dremotherium feignouxi*. The remains of rhinocerotids were reviewed by Becker (2003) and ascribed to *Diaceratherium lemanense*: some of them display derived morphological characters interpreted as probable intraspecific variations. These historic discoveries allow a first dating to the Aquitanian time.

During the construction of the Neufeld tunnel (2006–2008), the ancient fossil locality of Engehalde was made accessible for a restricted time. The Natural History Museum Bern organized a new palaeontological excavation campaign. The discovered material did not contain new rhinocerotid remains, but yielded essentially specimens of rumiants, composed by teeth and postcranial bones assigned to the "*Dremotherium*–like" group (probably *Dremotherium feignouxi*). The lower left jaw of a mustelid, probably from the genus *Palaeogale*, *Plesictis*, or *Plesiogale*, was the highlight of the new discoveries (Fig. 1). The washing and picking of sediment samples allowed the sorting of charophytes from the group *Stephanochara praeberdotensis* as well as small mammal remains with *Prolagus* sp., *Eucricetodon infralactorensis*, *Peridyromys* sp. and *Cainotherium* sp. (Menkveld-Gfeller & Becker 2008).

Figure 1. Lower left jaw of a mustelid-like predator (fossil length 6 cm)

These new data, in particular the occurence of *Prolagus* sp. and *Eucricetodon infralactorensis*, allow an improved dating of this locality to the late Aquitanian (European Mammal Reference Level MN2; Burkart Engesser, pers. com.). This biostratigraphical interpretation coincides with other well-dated localities reporting similar faunal composition, like the derived form of *Diaceratherium lemanense* (Becker et al. 2009) and the representatives of the *Amphitragulus elegans – Dremotherium feignouxi* group (Gentry et al. 1999). Regarding the palaeosynecology, the referred mammal association does not permit an accurate characterization of the environment of the Bern area during the late Aquitanian. However, the representatives of the *Amphitragulus elegans – Dremotherium feignouxi* group could point to the existence of a wooded environment. Their association with *Diaceratherium lemanense* underlines probably a bushland in a transitional zone between forest and grassland. Moreover, the lithofacies of the trapping sediments (fluvial sands and floodplain marls) indicate an environment probably close to bodies of water or swamps.

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6.2

Smithian ammonoids (Early Triassic): explosive evolutionary radiation following the Permian/Triassic mass extinction1

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In the aftermath of the end-Permian mass extinction, ammonoids were among the fastest clades to recover: the recent analysis of a global diversity data set of ammonoid genera from the Late Carboniferous to the Late Triassic shows that Triassic ammonoids actually reached levels of diversity higher than in the Permian less than 2 million years after the PTB (Brayard et al., 2009). The evolution of Early Triassic ammonoids was not a smooth, nor gradual process. It is characterized by the following main features: (i) a very low diversity in the Griesbachian (early Induan), (ii) a moderate diversity increase in the Dienerian (late Induan), (iii) an explosive radiation in the early Smithian (early Olenekian), (iv) a late Smithian extinction event followed by a second explosive radiation in the early Spathian (late Olenekian) (Brayard et al., 2006, 2009).

In order to better understand the Smithian ammonoid radiation we conducted extensive field studies in two classical regions for the Early Triassic, namely the Salt Range (Pakistan) and Spiti (Indian Himalayas). Smithian ammonoids from these regions have been known for more than a century, and these places are the type localities of many taxa (e.g. Waagen, 1895; Krafft & Diener, 1909). Additionally, we studied a section at Tulong (South Tibet) as well as extremely ammonoid-rich exotic blocks of Hallstatt Limestone in the Oman Mountains.

Our abundant, bed-rock-controlled and well-preserved material enables us to revise many classical ammonoid taxa that were previously known only inadequately. Moreover, a large number of new taxa was found, which enables us to define one new family, 18 new genera and about 29 new species. A total of eight successive ammonoid associations can be correlated between our sections (Brühwiler et al., 2007). This high-resolution biochronological scheme for the Smithian of the Northern Indian Margin can be correlated with ammonoid successions from other regions such as South China (Brayard & Bucher, 2008).

Due to the very high evolutionary rates of Early Triassic ammonoids (Brayard et al., 2009) the reconstruction of phylogenetic relationships among Smithian ammonoids is difficult. However, our well-constrained taxonomic and biochronologic data provide new insights on the evolution of several lineages. Furthermore, the ongoing comprehensive study of Dienerian ammonoid faunas from the Salt Range and from Spiti (Ware et al.) will help us to decifer the origin of some Smithian ammonoids.

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6.3

Darwinian dinosaurs : missing links or evolutionary failures ?

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Charles Darwin did not often mention dinosaurs in his works. In the third edition of *On the origin of species* (1861, p. 346), he alluded to them in a chapter about extinction: "So little is this subject understood, that I have heard surprise repeatedly expressed at such great monsters as the Mastodon and the more ancient Dinosaurians having become extinct; as if mere bodily strength gave victory in the battle of life. Mere size, on the contrary, would in some cases determine quicker extermination from the greater amount of requisite food". Ten years later, in *The descent of man, and selection in relation to sex* (1871, p. 204), he emphasized their evolutionary significance: "Prof. Huxley has made the remarkable discovery, confirmed by Mr. Cope and others, that the old Dinosaurians are intermediate in many important respects between certain reptiles and certain birds—the latter consisting of the ostrich-tribe (itself evidently a widely-diffused remnant of a larger group) and of the Archeopteryx, that strange Secondary bird having a long tail like that of the lizard".

Thus Darwin illustrated two views of dinosaurs that were to become both prevalent and competing until today: icons of extinction, or missing links. The "missing link" interpretation predominated during the last part of the 19th century and the beginning of the 20th, when dinosaurs were widely considered as ancestral to birds, on the basis of osteological resemblance and the discovery of both *Archaeopteryx* and the "toothed birds", *Hesperornis* and *Ichthyornis*, from the Late Cretaceous of the United States. According to this view, dinosaurs, as bird ancestors, had played an important part in the evolution of one of the most successful groups of living vertebrates. This interpretation fell out of favour during the mid-twentieth century, largely because of the influential book by Gerhard Heilmann, *The origin of birds* (1926), in which the purported absence of clavicles in dinosaurs was used to demonstrate that they could not possibly have been ancestral to birds (which possess clavicles) – since "Dollo's law" stipulates that once an organ has been lost in the course of evolution, it cannot reappear again.

As dinosaurs could no longer be seen as ancestral to anything, they had to be considered as some kind of evolutionary dead end, and this interpretation prevailed until the 1970s. The image of the dinosaurs as too large, too slow and too stupid to have been able to survive became prevalent for a large part of the 20th century. This could be seen in terms of natural selection, with large food requirements as a possible disadvantage, as already mentioned by Darwin in 1861, or in terms of non-Darwinian, orthogenetic evolution resulting in non-adaptive transformations detrimental to the organisms involved. The idea that dinosaurs were somehow "doomed" to extinction by rather obscure evolutionary mechanisms became popular for a long time.

Things changed again in the 1970s when dinosaur biology was thoroughly reinterpreted and the image of sluggish, cold-blooded giants was challenged and a new view of dinosaurs as more active, possibly warm-blooded, animals gradually emerged. This went together with a reappraisal of dinosaur-bird relationships, based on new discoveries of small carnivorous dinosaurs and descriptions of new specimens of *Archaeopteryx*, which resulted in a rebirth of the hypothesis of the dinosaurian ancestry of birds. This was strengthened by the discovery of clavicles in many dinosaurs (thus eliminating Heilmann's objection) and by that of the famous "feathered dinosaurs" from the Early Cretaceous of China, which provide extremely strong evidence in favour of a close phylogenetic relationship between small theropod dinosaurs and birds.

In the 1980s, the question of dinosaur extinction also underwent a revival, within the larger framework of catastrophic events at the Cretaceous-Tertiary boundary. The discovery of the major asteroid impact that happened 65 million years ago led to a thorough reconsideration of the possible causes of terminal Cretaceous extinctions, including that of non-avian dinosaurs. Seen as part of major extinction event affecting many groups of organisms in various environments, in all likelihood caused by the impact of an extra-terrestrial object, the disappearance of the dinosaurs could no longer be seen as the result of some mysterious inability to adapt to gradual environmental change. Although the details of dinosaur extinction at the end of the Cretaceous remain to be worked out, the reason for their disappearance is now much clearer than it was before the discovery of the end-Cretaceous impact – and Darwin's original remark about the importance of food resources (or the lack thereof) takes on a new significance in view of current hypotheses about the collapse of food webs following the asteroid impact.

Although the evolutionary significance of dinosaurs, both in terms of extinction and of intermediate forms, was apparent to Darwin, and to quite a few of his followers, including Huxley, in the 19th century, it was underrated during much of the 20th century. It is only since the 1990s that palaeontologists have recognised again that dinosaurs were not simply an extinct group of reptiles, but were in fact the source of one of the major groups of living vertebrates, viz. the birds, and that the demise of non-avian dinosaurs was the result of an exceptional global event, rather than the consequence of some kind of non-adaptive evolution. The example of dinosaurs illustrates well how the outdated concept of "evolutionary failures" has been superseded by a more truly Darwinian interpretation of the fossil record.

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6.4

Diatom assemblage turnover in the NW-Pacific at the 2.73 Ma climate transition

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The North Pacific contains a critical diatom sedimentary record of the Cenozoic global cooling history. The most striking part of that record covers the ultimate closure of the Panama Seaway 2.73 Ma ago which was synchronous with the onset of Northern Hemisphere glaciations (NHG). These physical changes were concomitant with an abrupt change in the biological pump efficiency related to the onset of ocean surface water stratification.
The ODP site 882 record (Leg 145) - with its well constrained Neogene paleoceanographic history around the 2.73 Ma transition - provides an excellent basis to test patterns and potential controls of diatom size variability and species dominance. Frustule sizes of centric diatoms have been quantified to better understand the environmental response of these organisms to a drastic and permanent paleoceanographic and climatic change.
Size and morphological characteristics of the centric diatom frustules (diameter >20 μm) were collected for a statistically representative number of specimens (i.e. 250-700) per sample using recently developed automated light microscopy and image analysis techniques.

6.5

Neogene global cooling: diatom size variability in a changing ocean

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Over the past 40 Ma, the development and stepwise expansion of the Antarctic ice-sheet, together with tectonic movements (e.g. closure of the Panama isthmus) have deeply modified the patterns of global circulation and chemical signature of the various water masses (e.g. redistribution of dissolved silica). These changes have also induced the development of oceanic boundaries (e.g. Polar front), directly affecting the evolution of planktic micro-organisms.
Using the widespread record of siliceous microfossils (Southern Ocean, Equatorial Pacific and North Pacific), we have assessed the impacts of these oceanographic reorganizations on diatoms, focusing on size and taxonomic changes and turnovers among centric diatoms over the past 15 Ma.
The ability of diatoms to adapt and survive in a changing ocean has probably been a key for their survival especially over the Neogene, when climatic and oceanographic changes have been the strongest. Similarly, size variability among this group tightly reflects their response to environmental perturbations as well as their taxonomic turnovers that have been driving diatom evolutionary patterns toward highly diverse and endemic communities prevailing in today's oceans.

6.6

Paleobiology of Early Triassic conodonts: implications of newly discovered fused clusters imaged by X-ray synchrotron microtomography

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Several fused clusters of conodont elements of the Early Triassic genus *Novispathodus* were discovered in limestone beds at the Smithian-Spathian boundary (Luolou Formation., Galfetti *et al*., 2008) from several localities within the Guangxi province of South China. Conodont clusters are groups of morphologically different elements belonging to the same individual, which were somehow cemented together post-mortem. Such specimens of exceptional preservation are extremely rare in the Triassic and these are the first reported for the Early Triassic.

Our fused clusters partially preserve the relative three-dimensional position and orientation of some ramiform, grasping elements. They are therefore extremely important for our understanding of the feeding apparatuses of conodonts.

Because of the intricate geometry of the superposed elements, of their fragility and of their extreme rarity, it is usually tricky to study such specimens. We overcome these problems by performing a propagation phase contrast synchrotron microtomography (Tafforeau *et al*., 2006). A pink beam setup at 17.6 keV, which was very recently developed at the European Synchrotron Radiation Facility on beamline ID19, has been successfully tested on our conodonts. This new technique enables a submicron resolution (0.23µm) with a speed and an overall quality never reached before. Some fused clusters as well as co-occurring isolated elements from the same sample and pertaining to the same multi-element species were scanned using this technique.

Besides taxonomic revision of the Gondolelloidea superfamily (the most significant group of conodonts during Permian and Triassic times), this discovery led us to propose a new functional model.

In our view, the best solution implies the presence of a presumably cartilaginous 'copula', upon which the conodont elements are moving independently, more or less as do dental plates in extant lampreys, but not strictly as proposed by Purnell and Donoghue (1997). We suggest that during retraction towards the caudally located platform (cutting or grinding) elements, the S0 element first has a closing, rotating movement, most probably synchronized with the closure of the M elements, with which it would have performed a pinching, seizing function. This movement is then followed by a sub-straight, dorso-caudally directed translation, by which it would have torn off the prey's 'flesh' and brought it towards the platform elements. The latter movement is accompanied by the closure of the other S elements, channelling the food in the appropriate direction.

Considering that the presence of such 'copula' associated with tongue protractor and retractor muscles has been asserted only for extant cyclostomes (hagfishes and lampreys; Yalden, 1985; Donoghue *et al*., 2000), our new model may provide important insights for deciphering the affinity of conodonts and for our general understanding of the origin of vertebrates.

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Figure 1. Animated 3d reconstruction of the feeding apparatus of Novispathodus.

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6.7

The Devonian Nekton Revolution

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Impressive discoveries of Neoproterozoic and Early Palaeozoic Fossillagerstaetten drew the attention on evolutionary and ecological processes of these timespans. It almost seemed that, except for some of the "Big Five", nothing essential happened after the Ordovician. Such a scenario is certainly not true.

Contrariwise, some major ecological fluctuations have been recorded from the Devonian, several of which have less prominent Silurian precursors. Famous examples are the radiation of land plants and jawed fish (both known already from the pre-Devonian). During the Devonian, several animal groups conquered the land (various arthropods and possibly tetrapods). Marine invertebrates show significant ecological and morphological changes: Important cephalopod groups such as bactritoids as well as ammonoids evolved and reef growth increased until the Late Devonian crises. Both the global rise and fall of dacryoconarids occurred, graptolites became extinct, and various mollusc clades modified early ontogenetic strategies during the Devonian, documenting a planktonic turnover. In addition, there is a macroecological change in marine faunas from a demersal (swimming close to the sea-floor) and planktonic habit towards a more active nektonic habit.

Various interpretations are at hand to explain this Devonian Nekton Revolution: (1) Demersal and nektonic modes of life were probably initially driven by competition in the diversity-saturated benthic habitats as well as (2) the availability of rich planktonic food resources (as reflected in evolutionary alterations in early ontogenetic stages of many mollusks). Escalatory feedbacks probably promoted the rapid evolution of nekton (jawed fish and some derived cephalopod groups in particular) in the Devonian, as suggested by the sequence and tempo of water-column occupation. Potentially, both these radiations and the Givetian to Famennian mass-extinctions were linked to a pronounced increase in nutrient input to sea surface waters during eutrophication episodes.

6.8

Red trilobites with green eyes from the Devonian of Morocco

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Latest Emsian (Early Devonian) sediments at the famous mud-mound- and trilobite-locality Hamar Laghdad (Tafilalt, Morocco) yielded some well preserved, largely red-coloured remains of phacopid trilobites. Closer examination revealed that only the lenses of the eyes of these phacopids are usually greenish in colour. EDX-analyses showed that the lenses retained their original calcitic composition while most of the exoskeleton was silicified. The silicified parts contain elevated concentrations of iron which causes the red colour.

Presumably, the primary porosity of most of the phacopid exoskeleton except the chitinous legs and the lenses was, because of the pore canals, higher than that of the lenses, facilitating the replacement of calcite by other minerals. Furthermore, the presence of organic components in the lenses in combination with a homogeneous distribution of the calcite crystals might have slightly increased the resistance of the lenses towards mineral replacement. The homogeneity of the calcite crystals of the lenses was needed for their optimal optical functionality. These factors probably account for the fact that the eyes retained the calcite which is often greenish in brachiopod shells such as the thick-shelled Middle Devonian *Devonogypa* and *Ivdelinia* from the Maïder Basin while the rest of the trilobite exoskeleton is red. This differential replacement also explains why the lenses are slightly corroded while the rest of the exoskeleton is superficially well preserved. So far, this differential replacement of calcite is only known from the eyes of phacopids. Other trilobite taxa from the same strata and locality have holochroal eyes and thus much smaller lenses which were probably more rapidly replaced by silica. The greenish colour of the lenses might originate from impurities of iron and magnesium; the concentrations of the corresponding ions might have been too low to be detected with the EDX with certainty.

Hamar Laghdad also yielded phacopid exoskeletons with less completely silicified exoskeletons which enabled a detailed reconstruction of the silicification process. Initially, only the outer surface of the exoskeleton and the vicinity of pore canals were silicified. In a second step, the bend in the growth lines of the interlensar sclera were silicified together with the remaining exoskeleton except for the lenses, then the complete interlensar sclera and in the end also the lenses.

6.9

First record of a belemnite preserved with beaks, arms and ink sac from the Nusplingen Lithographic Limestone (Kimmeridgian, SW Germany)

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A recent discovery of an unusually preserved belemnite from Nusplingen comprises the extraordinarily rare remains of beaks and nearly *in situ* arm-hooks as well as the ink sac and the incomplete phragmocone. So far, *Hibolithes semisulcatus* (Münster, 1830) is the only larger belemnite known from the Nusplingen Lithographic Limestone (Upper Jurassic, Late Kimmeridgian, Beckeri Zone, Ulmense Subzone; SW Germany) which has the same phragmocone shape and size, thus we assign the new specimen to this taxon. The rostrum was probably lost due to a lethal predation attempt in which the prey was killed but not entirely eaten. For the first time, a specimen reveals details of the belemnite beak morphology, which we compare to the beaks of other Jurassic cephalopods. This specimen presently represents the only known rostrum-bearing belemnite of post-Toarcian age which has been preserved with non-mineralised body parts. As *Hibolithes semisulcatus* is known to possess one pair of mega-onychites, the absence of those in the present specimen provides evidence of sexual dimorphism in *Hibolithes semisulcatus.* This phenomenon was previously presumed for all belemnites, but it is known only from *Passaloteuthis* with certainty since the rostrum of the latter is unambiguously associated with an arm crown that occasionally includes one pair of mega-onychites. The imperfect preservation of the belemnite beaks hampers a detailed comparison with other Recent and fossil coleoid beaks. Some morphological characters (low width of the outer lamella, double lateral lobes of the dark parts of rostrum and hood, possibly short internal lamella) of the lower beak of *Hibolithes* more closely resemble Recent decapods than Recent octopods. The upper beak of *Hibolithes* differs in the long, narrow and curved rostrum from those coleoid beaks previously known from Nusplingen. The dark part of the lower beak also shows a unique outline with a short and pointed rostrum, an elongate posteroventral extension and two small rounded sinuses which pointed towards the wings (sometimes similarly developed in Recent *Sepioteuthis*). It appears likely that this beak form is quite characteristic and it might reflect a special diet of the belemnites. Taking their probably high swimming velocity (fins, stream-lined body, and horizontal orientation of the longest body axis) with the arm hooks and the sharp beaks into account, it appears quite likely that belemnites were fast-swimming, effective, medium-sized predators. With the new discovery, Nusplingen now represents the only locality which has yielded complete beak apparatuses from all major Jurassic cephalopod groups.

6.10

The borehole 01983X2854 (Preuschdorf, Upper Rhine Graben, Alsace, France) as a basis of a formal definition of the Upper Pechelbronn Beds (Rupelian)

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From the middle Eocene to Late Oligocene, an intense lacustrine, brackish and marine sedimentation, documented by salt deposits and oil accumulation, took place in the Upper Rhine Graben (URG), especially in the Pechelbronn Beds (Lower-, Middle- and Upper).

Although these layers were studied, in the past, for the oil industry (Schnaebele 1948) and are a lithostratigraphic unit used in maps and papers concerning the Paleogene of the URG, they have never been formally designated because they almost never crop out at the surface and drifting and drilling materials were often discarded. Nevertheless, the International Stratigraphic Guide (see Murphy and Salvador 1999), demands a type section for each formally named Formation.

Several palaeogeographical reconstitutions and stratigraphic charts for the URG have been published (Berger et al. 2005 a & b). However, the Rupelian deposits were not well defined.

This work presents the first step for a definition of a type section of a type section of the Upper Pechelbronn Beds, with the presentation of several lithofacies and paleontological data.

The studied borehole, 01983X2854 (Preuschdorf, Alsace, France) is a complete cored drilling, about 220m in depth. It was originally made to evaluate a decontamination issue, but has also yielded micropaleontological and sedimentological data. It corresponds to the Upper Pechelbronn Beds with a small part of the Middle Pechelbronn Beds at the base.

The high abundance of ostracods and gastropods in grey marls, corresponding to the 10 lower meters, indicate the top of the Middle Pechelbronn Beds with the Hydrobia Zone. These layers are covered by a succession of marls and sandstone, suggesting a different environment. The lower part of the borehole is consistent with the lithostratigraphic zonation defined by Schnaebele (1948) for his “normal facies” whereas the upper part corresponds to his “freshwater facies”.

The lower part of the borehole has yielded new paleontological data. Diatoms (*Triceratium* sp), charophytes (*Chara* spp., *Rhabdochara* sp.), foraminifers (*Ammodiscus* sp., *Quinqueloculina* sp., *Flintina* sp., *Lenticulina* spp., *Dentalina* sp., *Subreophax elongates*, *Vaginulopsis* spp.), bivalves, gastropods, bryozoans, ostracods (*Grinioneis tribeli*, *Hazelina indigena*, *Hemicyprideis* spp., *Ilyocypris* sp.), insects, echinoderms, fishes and mammals teeth are used as main indicators of biostratigraphy and palaeoecology. The fossil record emphasizes a complex alternation of freshwater, brackish and marine fauna along the whole studied section.

This study is financed by the SNF Project 200020-118025 “Paleontology and Stratigraphy of the Rhine graben during the Paleogene”, and includes parts of the Masters-thesis of B. Yerly “ The transition between the Middle and Upper Pechelbronn Beds in the drilling 1983X2854, Preuschdorf (Rupelian, Upper Rhine Graben, Alsace, France)” (in prep. 2009) and the PhD-thesis of T. Lavoyer “Paleontology and Stratigraphy of the Middle Upper Rhine Graben during the Paleogene: a key-study for the relationships between Rift system, Alpine Orogeny and Paleoclimate” (in progress).

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6.11

Determination of the paleodiet and the phylogeny of extinct ruminants using Relative Wrap Analysis on mandibles: case of Iberomeryx minor (Mammalia, Artiodactyla)

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The primitive ruminant *Iberomeryx* is essentially known by few dental remains and is still poorly documented. Its phylogeny and palaeobiology stays rather enigmatic. Only two species have been described: the type species *I. parvus* from the Benara locality in Georgia (Gabounia 1966), and the West European species *I. minor* from Itardies, Mounayne, Raynal and Roqueprune 2 in Quercy (Sudre 1987), Montalban in Spain (Golpe-Posse 1974), and Lovagny, Soulce and Beuchille in the Swiss Molasse Basin (Becker et al. 2004). *I. savagei* from India had recently been placed in the new genus *Nalameryx* (Métais et al. 2009). All these localities are dated to the Rupelian and correspond mainly to MP23 (European mammal biozone). Based on the short tooth-crown height and the bunoselenodont pattern of the molars, Sudre (1984) and Becker et al. (2004) proposed a folivore/frugivore diet for *Iberomeryx*.

Based on relative warp analysis (24 landmarks) of 84 extant and fossil ruminant mandibles from 24 genera and 32 species, this study proposes a preliminary discussion on the phylogeny and the diet of the genus *Iberomeryx*. The results permit to differentiate *Pecora* and *Tragulina* on the first axis thanks to the length of the diastema, the length of the premolars and the mandible ankle. As suggested by Sudre (1984), *Iberomeryx* is close to the extant Tragulina by the shape of its mandible. But, this latter is clearly different of those of the Tragulidae, the only extant family in Tragulina. This difference is essentially due to a stockier mandible (condylar process, mandible ramus and *corpus mandibulae*), and a deeper mandibular incisure. Additionally, we observe no diastema and well bunodont teeth. *Iberomeryx* may be considered as a primitive Tragulidae, the only known from the Oligocene, based on the general shape of its mandible and its jaw teeth. Moreover, its diet could not be strictly frugivore, but it could possibly also exceptionally eat some meat matter such as small Hypertragulidae.

This study is supported by the Section d'archéologie et paléontologie (Porrentruy), the University of Fribourg, and the Swiss National Foundation project (115995) on the large mammal evolution in the Swiss Molasse Basin during the Oligocene and Early Miocene.

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6.12

Macroevolutionary trends of Acrochordiceratidae Arthaber, 1911 (Ammonoidea, Middle Triassic)

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Directed evolution of life through millions of years, such as increasing complexity and increasing adult body size, is one of the most intriguing patterns displayed by fossil lineages. The general tendency for body size to increase during the evolution of a group of animals is known as Cope's rule. Processes and causes of such macroevolutionary trends remain however to be clearly understood (Jablonski 2000). Among fossils, ammonoid shells (marine cephalopods) are well known to experience repetitive macroevolutionary trends of their adult size, geometry and ornamentation (Schindewolf 1940; Haas 1942; Bayer & McGhee 1984; Dommergues 1990; Guex 1992).

This study analyzes the evolutionary trends of the family Acrochordiceratidae Arthaber, 1911, which spanned the upper Early to lower Middle Triassic. Exceptionally large collections of this ammonoid family from North America enable quantitative and statistical analyses of its macroevolutionary trends. This study highlights that (1) the monophyletic clade of Acrochordiceratidae follows the classical evolute to involute evolutionary trend (i.e. increasing coiling of the shell); (2) the lineage also shows a seemingly stepwise increase of its shell adult size (shell diameter); (3) the clade also records increasing complexity of its suture line; and (4) the lineage is also characterized by a prominent increase of the intraspecific variation of its shell morphology, which follows the Buckman's Law of Covariation.

These macroevolutionary trends are statistically robust and seem more or less gradual. Furthermore, they can be considered as non-random with the sustained shift of the mean, the minimum and the maximum of studied shell characters. Such result is usually interpreted as being the effect of a selection pressure on the entire lineage, which leads to infer the presence of one ecological niche common to all species of this mostly anagenetic lineage with moderate evolutionary rates.

Increasing involution of ammonites is usually interpreted by increasing adaptation mostly in terms of improving hydrodynamics. However, this trend in ammonoid geometry can be explained as a case of Cope's rule (increasing adult body size) instead of *ad hoc* functional explanations of coiling, because both shell diameter and shell involution are two possible paths for ammonoids to accommodate increasing body size.

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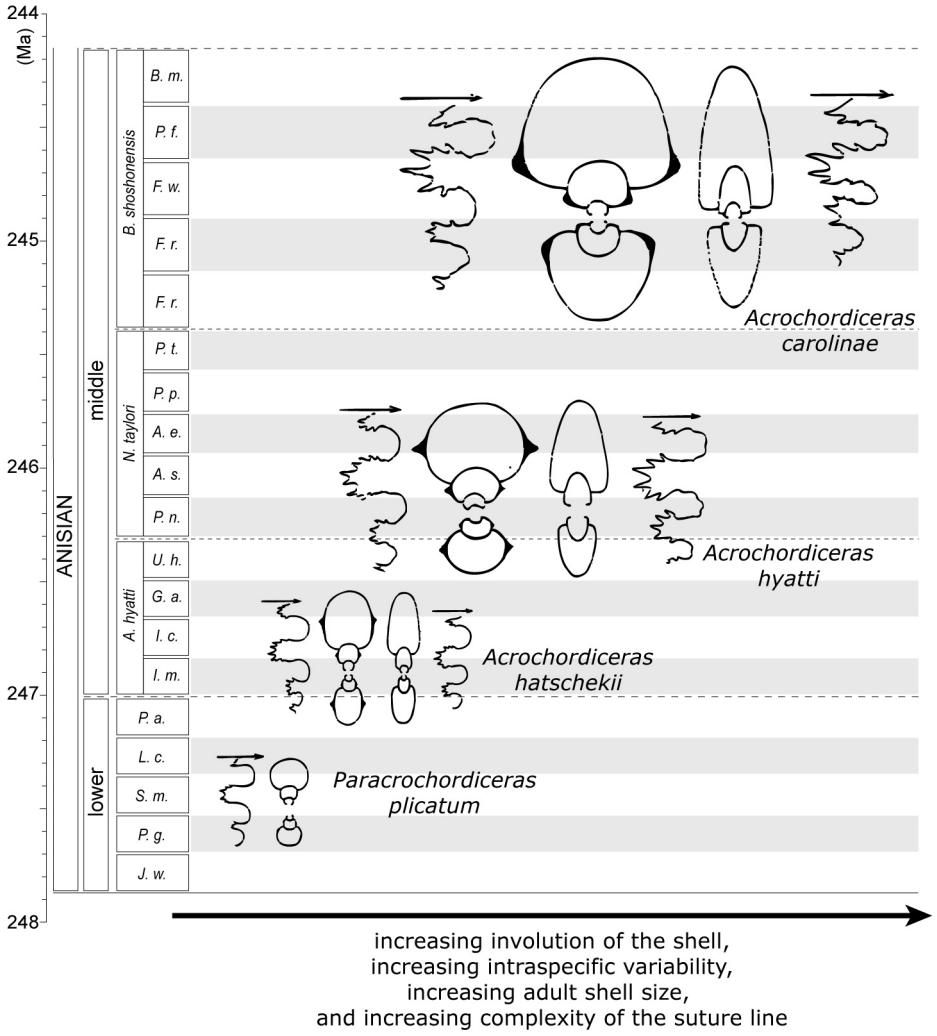
Figure. Evolutionary trends represented by late immature shell geometry and suture line for Acrochordiceratidae during the Anisian (Middle Triassic). Global evolutionary trends affecting successive spectra of variants for Acrochordiceratidae are increasing adult shell size, increasing involution, increasing suture complexity, and increasing intraspecific variability. (Next Page)



6.13

Reinvestigation of the basal ray-finned fish Birgeria stensioei from the Middle Triassic of Monte San Giorgio (Switzerland) and Besano (Italy)

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The two earlier descriptions and a previous reconstruction of the Middle Triassic actinopterygian *Birgeria stensioei* Aldinger, 1931 from the Besano Formation of Monte San Giorgio (Canton Ticino, Switzerland) and Besano (Lombardy, Italy) relied either on a few fragmentary remains or on a single individual only. Here we present the first study of *B. stensioei* that is based on multiple specimens of this basal ray-finned fish. Sixty-seven specimens have been examined.

The reinvestigation of *B. stensioei* yielded new information at genus and species level. *B. stensioei* predominantly differs from the other species of the genus *Birgeria* Stensiö, 1919 in the arrangement of the bones of the dorsal fin base. While in the other species usually two series of pterygiophores are present throughout the dorsal fin base, only one series of pterygiophores is developed in the anterior part of the dorsal fin root of *B. stensioei*. The caudal peduncle and the caudal fin lobes are more slender and longer than illustrated in the previous reconstruction of *B. stensioei* (see Schwarz 1970). The morphology of the caudal peduncle and fin as well as the aforementioned specialised dorsal fin root indicate that propulsion might have been more advanced in *B. stensioei* compared to the other species of the genus *Birgeria*. *B. stensioei* is furthermore distinguished from most of the other species of *Birgeria* by the degree of ossification of the brain case and the palatoquadrate. As in many other basal actinopterygians, a dermohyal is developed in *B. stensioei* and this bone is probably present in the other species of *Birgeria* as well.

6.14

Terrestrial palaeoclimatical and palaeoenvironmental reconstructions in Northwestern Switzerland: carbon and oxygen isotope compositions of Early Oligocene and Late Pleistocene vertebrate remains.

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Vertebrate remains from two Early Oligocene localities of the Delémont basin (Beuchille and Poillat) and from eight Late Pleistocene doline fillings of the Ajoie Region (Courtedoux-Vâ Tche Tchâ and Boncourt-Grand'Combe) have been excavated along the Transjurane highway (Canton Jura, Northwestern Switzerland). Teeth of large mammals and bones of aquatic reptiles have been analysed for their isotope compositions ($\delta^{18}O_{CO3}$, $\delta^{18}O_{PO4,}$ $\delta^{13}C$) in order to reconstruct the palaeoclimatical and palaeoenvironmental conditions.

The two Early Oligocene localities of Beuchille and Poillat are located in the Jura Molasse ("Molasse alsacienne" Formation) of the Delémont basin (Northern Switzerland). The presence of the small mammal *Blainvillimys avus* and the ruminant *Iberomeryx minor* allows a datation to the mammal zones MP23-24, around 31.5 to 29.0 Ma (Becker et al. 2004). Eight samples of reptile bones (crocodiles and turtles) as well as four samples of sympatric primitive rhinocerotid teeth (*Ronzotherium* sp.) have been analysed. The reptile bones have low $\delta^{18}O_{PO4}$ values (from 13.6‰ to 17.8‰) indicating freshwater environments ($\delta^{18}O_{H2O}$ calculated values averaging -6.15±1.03‰) which are supported by the palaeontological identifications of the turtle remains (*Trionyx* and Testudinidae: freshwater and terrestrial turtles, respectively). A similar $\delta^{18}O_{H2O}$ value of -6.18±1.5‰ is calculated from enamel $\delta^{18}O_{PO4}$ values (18.3±1.3‰) of the rhinocerotid teeth, which presumably reflects the composition of meteoric water. Using a modern-day mean air temperature (MAT)-$\delta^{18}O_{H2O}$ relation for Switzerland a MAT of 18.0±2.5°C for the Early Oligocene could be calculated and was about 8-9°C warmer than today in the Canton Jura (Recent MAT of 8.7°C). This result is in agreement with the palaeotemperature of ~17°C reconstructed from fossil plant remains in the Early Oligocene of Central Europe by Mosbrugger et al. (2005).

The eight Late Pleistocene doline fillings of Boncourt-Grand'Combe (GC) and Courtedoux-Vâ Tche Tchâ (VTA) are located in the Ajoie Region (Northwestern Switzerland) and correspond mainly to loessic and gravel deposits associated with fossil remains. Forty-six teeth of large mammals (*Equus germanicus, Mammuthus primigenius, Coelodonta antiquitatis, Bison priscus*) have been analysed: eight samples from the GC doline filling and thirty-eight from the seven VTA doline fillings. The sedimentary series bearing the mammal remains trapped within the GC doline have been dated by OSL (Optically Stimulated Luminescence) to an age of ~80 ka BP. The mammal remains preserved within the seven VTA dolines have all been discovered in the same sedimentary unit dated to the time interval 45-40 to 35 ka BP (latest Middle Pleniglacial) by OSL and radiocarbon (Becker et al. 2009).

According to the enamel $\delta^{13}C$ values, which are similar in both time periods, the large mammals lived in a C_3 plant-dominated environment as indicated by values ranging from -14.5‰ to -9.2‰ (O'Leary, 1981). The MAT calculated from the $\delta^{18}O_{PO4}$ values of the large mammal assemblage from the GC doline averages 6.0±4.6°C. The MAT calculated for the large mammal assemblage of the younger VTA dolines averages 5.6±4.1°C, showing a quite similar climate. This latter result is concording with the quantified ecology study of the small mammal assemblages of these dolines, which indicates palaeotemperatures averaging 5°C (Oppliger, 2009). These palaeoclimatical values are about 3 to 4°C cooler than today in the Canton Jura. However, some variations in the $\delta^{18}O_{PO4}$ values of the different studied species are observed, and particularly in the VTA dolines: for example the equids show slightly lower $\delta^{18}O_{PO4}$ values (13.09±0.8‰) than the bovids (14.6±1.1‰). The calculated MAT after specific calibrations can thus be very different, ranging from 2.2±2.8°C for the *Equus* remains to 8.8±3.5°C for the *Bison* remains, with a value of 5.8±3.3°C for the *Coelodonta* and 8.7±2.2°C for the *Mammuthus*.

In order to understand this bias a precised sampling of teeth formed before and after the weaning of the foals has been done. It shows that the oxygen isotopic compositions are not affected by the nursing period whereas the carbon isotopes show slightly lower values. The differences in oxygen stable isotope compositions within these Late Pleistocene mammals could then been explained by the sampling method, the mammal physiology and/or ecology, or time averaging. The determination of a palaeotemperature should be more reliable during the Oligocene when the climate was much more stable than in the Pleistocene when brutal climatical changes occurred very frequently.

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6.15

How do recurrent patterns of covariation in molluscan shells connect to growth dynamics?

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The comparison of shell shape among and within different clades of molluscs can be informative with regards to the basic rules of accretionary growth. Indeed, patterns of variation of shell shape and its associated growth features (like growth halts) in ammonoids and gastropods suggest that common rules of accretionary growth underlie the morphogenesis of the shell and its evolution in both clades (e.g. Bucher, 1997; Checa & Jimenez-Jimenez, 1997; Checa et al. 2002).
Moreover, in some phylogenetically distant ammonoids species, covariations among the intensity of ornamentation, the lateral compression of the aperture and the degree of whorl overlap have been described (Buckman's laws). It has been suggested that simple growth rules could underlie these evolutionary recurrent patterns of covariation (Hammer & Bucher, 2005a). Similarly, shell characters covary with the spacing between growth halts during the ontogeny of some of these highly variable ammonoids species.
One goal of this study is to explore whether a comparable pattern of covariation is to be found in gastropods as well. We also want to find out whether documentation of modes of growth in gastropods could support the view according to which some recurrent patterns of covariation could reflect basic constraints tied to accretionary growth. Another interest is the relationship among shape, growth rates and age, a point that is difficult, if not impossible to study on ammonoids.
In this study, we investigate the ontogenetic patterns of covariation among aperture shape, intensity of ornamentation and spacing between growth halts in a population of gastropods (*Hexaplex trunculus*, Muricidae) reared under controlled laboratory conditions. All individuals originated from a single egg mass. We describe the growth dynamics of these individuals from the age of approximately 100 days to 550 days after hatching.
This study highlights a covariation among growth rhythm, growth halts spacing, aperture allometry and intensity of ornamentation:
-Variation in shell shape is analysed by geometric morphometrics of landmarks located on the aperture. We document an ontogenetic allometry of aperture, which becomes relatively wider with size. This is consistent with results obtained using elliptic Fourier analysis of aperture contour and traditional biometrics.
-Variation in the 'strength of ornamentation' is related to the mean spacing between growth halts: smoother snails tend to exhibit more closely spaced growth halts. This covariation, as put in evidence here in *H. trunculus*, seems analogous to that observed in some highly variable ammonoids species (e.g. *Gymnotoceras rotelliformis*, *Amaltheus margaritatus*).
-The mean number of growth halts per month is related to the global shape of the growth curve and to the mean spacing between growth halts: the more frequent the growth 'pulses', the shorter the time spent on a growth halt (down to nearly continuous growth), the more linear the growth curve and the smaller the growth segments between successive growth halts.
Additionally, we develop a growth vector model (Urdy et al., 2009) in order to simulate the formation of growth halts phenomenologically (Fig.1). This model is able to account for some patterns of covariation among specimens. In particular, variation in growth rhythm is regarded as critical in generating the observed covariation between growth halts spacing and ornamentation. Based on these simulations, we suggest that this covariation mainly results from simple scaling among the aperture dimensions and the lengths of shell segments between successive growth halts. Then, the important structuration of phenotypic variation in some ammonoids species could be a generic outcome of underlying variation in growth rhythm.

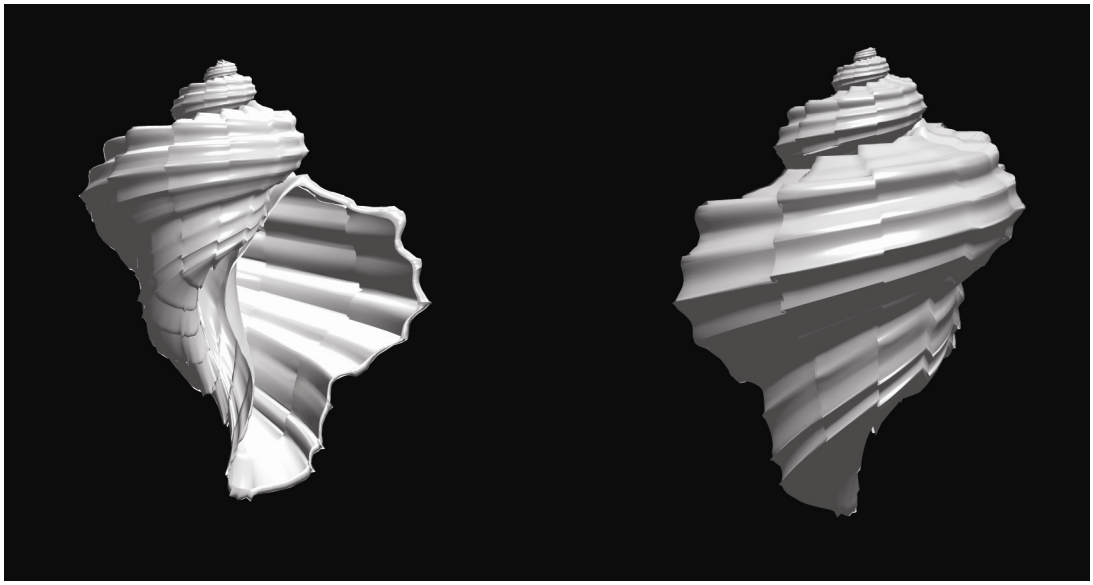

Figure 1: Example of a simulation of growth halts.

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